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Wave exposure shapes reef community composition and recovery trajectories at a remote coral atoll

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Abstract

In a time of unprecedented ecological change, understanding natural biophysical relationships between reef resilience and physical drivers is of increasing importance. This study evaluates how wave forcing structures coral reef benthic community composition and recovery trajectories after the major 2015/2016 bleaching event in the remote Chagos Archipelago, Indian Ocean. Benthic cover and substrate rugosity were quantified from digital imagery at 23 fore reef sites around a small coral atoll (Salomon) in 2020 and compared to data from a similar survey in 2006 and opportunistic surveys in intermediate years. Cluster analysis and principal component analysis show strong separation of community composition between exposed (modelled wave exposure >1000 J m^{-3}) and sheltered sites (<1000 J m^{-3}) in 2020. Differences are driven by relatively high cover of *Porites* sp., other massive corals, encrusting corals, soft corals, rubble and dead table corals at sheltered sites versus high cover of pavement and sponges at exposed sites. Total coral cover and rugosity were also higher at sheltered sites. Adding data from previous years shows benthic community shifts from distinct exposure-driven assemblages and high live coral cover in 2006 towards dominance of bare pavement, dead *Acropora* tables and rubble after the 2015/2016 bleaching event. The subsequent, and still ongoing, recovery trajectories at sheltered and exposed sites are surprisingly parallel and lead communities towards their respective pre-bleaching communities. These results demonstrate that in the absence of human stressors, community patterns on fore reefs are strongly controlled by wave exposure, even during and after widespread coral loss from bleaching events.

Introduction

Coral reef structure, function and resilience are influenced by a combination of physical and anthropogenic drivers. As reefs worldwide are degrading and shifting to alternative regimes (Pandolfi et al. 2003; Norström et al. 2009), and climate-driven bleaching events are increasing in frequency and severity (Hoegh-Guldberg 1999; Hughes et al. 2018), the understanding of these drivers in shaping reef communities and supporting recovery after disturbances is of vital importance (Hughes et al. 2010; Pandolfi et al. 2011; Page et al. 2019). Physical drivers of reef communities include wave forcing, temperature, nutrients, primary production and turbidity (Robinson et al. 2018; Wedding et al. 2018; Ceccarelli et al. 2020), often in turn shaped by spatial gradients in waves, currents and local bathymetry.

Spatial gradients in wave energy strongly influence benthic and fish community patterns at the scale of individual islands and coral atolls (Williams et al. 2013; Jouffray et al. 2019; Karkarey et al. 2020). For instance, high wave forcing can reduce overall coral cover and favour wave-tolerant morphologies, such as encrusting corals (Dollar 1982; Storlazzi et al. 2005; Franklin et al. 2013) or may even shift the entire benthic community to a dominance by low-lying algal species, such as turf algae and crustose coralline algae (CCA) (Williams et al. 2013; Gove et al. 2015). Coral vulnerability to high wave energy is mainly determined by colony morphotype and size, with large corymbose or table corals experiencing high mortality through hydrodynamic dislodgement (Madin and Connolly 2006; Madin et al. 2014). After a disturbance, hydrodynamic forces can furthermore affect the rate at which new coral habitat is formed and old coral habitat degrades (Madin et al. 2016), potentially influencing recovery trajectories. Anthropogenic drivers such as fishing and coastal development lead to sedimentation, nutrient enrichment and overfishing of herbivores (McManus et al. 2000; Fabricius 2005) which can initiate shifts to different reef regimes (Hughes 1994; McCook 1999; Jouffray et al. 2019) and decouple natural relationships between reef assemblages and physical drivers (Williams et al. 2015; Ford et al. 2020).

To disentangle effects of anthropogenic and physical drivers, remote reefs are invaluable places to study impacts of natural environmental gradients in the absence of direct human disturbance (Gilmour et al. 2013; Hays et al. 2020). However, remote areas are often associated with access limitations, leading to sparse temporal and spatial data resolution. In order to evaluate the status and recovery potential of reef communities on a meaningful scale, strategic monitoring over large areas and with high spatial resolution is necessary. This study evaluates how wave exposure structures coral reef benthic community composition and recovery trajectories after a major bleaching event in the remote Chagos Archipelago, Indian Ocean. In 2020, 23 fore reef sites around the entire Salomon atoll were surveyed to address the following question: 1) Does benthic community structure around the atoll vary predictably based on wave exposure? Average community compositions at sheltered and exposed sites were then compared to cover data in 2006 and intervening years to explore the subsequent question: 2) Are pre-bleaching status and recovery trajectories after the 2015/2016 disturbance event impacted by wave exposure? The results increase our understanding of wave exposure as a driver of reef ecology in remote atolls and its effects on recovery trajectories after major disturbance events.

Methods

Study site and wave exposure

The Chagos Archipelago in the central Indian Ocean consists of five atolls with islands and numerous submerged banks. All atolls, except for Diego Garcia, have been uninhabited since the 1970s and have therefore experienced minimal direct or local impacts from fishing, sewage or shoreline modifications for the last 50 years (Sheppard et al. 2017). In 2010, the Archipelago and surrounding sea was declared one of the largest no-take marine protected areas, benefitting benthic and pelagic ecosystems alike (Hays et al. 2020). However, despite minimal local impacts, two major global heating events in 1997/1998 and 2015/2016 reduced coral cover values from >40 to <10% across the Archipelago and affected reefs down to 25 m water depth (Sheppard et al. 2017; Head et al. 2019). Coral reefs recovered to pre-bleaching levels 7-10 years after the 1997/1998 event, while recovery after 2015/2016 is currently ongoing (Sheppard et al. 2017). Due to the remoteness of the Archipelago and related access limitations, research effort has strongly focused on repeat monitoring of the same sites to build a time-series of observations, while most areas remain understudied. Salomon atoll is located in the northeast of the Chagos Archipelago, covering approximately 38 km^2 (Fig. 1a). A reef crest and 10 small islands enclose a shallow lagoon (<30 m depth), harbouring sheltered backreef and coral knoll habitats. The fore reef terrace surrounds the whole atoll and gently slopes from 3 to ~10 m depth before dropping off steeply, with a passage to the lagoon on the northern side (Fig. 1c).

The seasonally-shifting wind regime in the central Indian Ocean, with the predominant wind direction being from the south-east (Fig. 1d), results in marked spatial variations in wave energy around the atoll. Wave exposure at each site was modelled as a function of wind speed, wind direction, and fetch length (i.e. the distance over open ocean that wind can travel in a specific direction unobstructed by land or reefs) using a model developed for a previous study (detailed information in supplementary material of Perry et al. 2015). Based on the model outputs (Fig. 1b) and a natural break in the rank order of data, sites were classified into 'exposed' (>1000 J m^{-3}), encompassing northeast and southeast facing shores, or 'sheltered' (<1000 J m^{-3}), encompassing southwest and northwest facing shores. We suspect that sites at the NE margin might have slightly lower wave exposure than calculated by the model, as the prominent current runs along-shelf and has to cross larger distances over the length of the reef terrace, but available bathymetry data prevents the model factoring for this.

Benthic community composition 2020

To determine whether benthic community structure around the atoll varies predictably based on wave exposure, a detailed survey of Salomon's fore reefs was conducted on 22 March 2020 by circumnavigating the atoll in a clockwise direction. The 23 sites (Fig. 1b) were chosen prior to the survey by placing GPS waypoints on a map at 1 km distance from each other. At each site, the depth of the reef terrace was checked with a handheld Echotest 2 depth sounder and the survey location adjusted to 6-8 m water depth. Two observers took planar photographs of the reef substrate from the surface and from ~3 m distance to the benthos by swimming and duck diving on a parallel transect to the reef crest in opposite directions, with a spacing of >3 m between photographs to ensure independence of replicates. Both observers used Canon Powershot G7X in underwater housings, automatic underwater mode and raw image quality. A third observer took short videos of the substrate at an oblique angle to evaluate the rugosity at each site, which was rated on a scale of 1-5 (5 = highest complexity) by three independent observers and averaged.

The photographs taken from approximately 3 m above the reef surface (n=10/site, 230 total) were uploaded to CoralNet (www.coralnet.ucsd.edu), a web-based tool for coral reef analysis supporting semi-automated annotation of images (Beijbom et al. 2015). Fifty random points were projected on each photograph (excluding the outer 10% of the image to avoid any blurry areas caused by camera distortion) and the substrate directly below was identified to scleractinian coral genus and morphotype level (Acropora_table, Acropora_branching, Pocillopora_branching, Stylophora_branching, Other_branching, Porites_massive, Other_massive, All_encrusting), or to other categories of benthic substrate (Soft coral, Sponge, Sand, Rubble, Dead_Acropora_table, Pavement, Halimeda, Other_Macroalgae). Note that Pavement includes cover of crustose coralline algae (CCA) and fine turf algae, which were not easily distinguishable in the photographs. The percent cover data for each picture were downloaded and some categories were combined due to very small values (Pocillopora + Stylophora + Other_branching = Other_branching; Halimeda + Other_Macroalgae = Macroalgae). Cover values were averaged over replicates at each site to yield site-level data (accessible at doi – [*data table attached, will be deposited in repository upon acceptance*]).

To evaluate differences in community composition we used the beta diversity metric Bray-Curtis on log transformed cover data. Hierarchical agglomerative clustering (CLUSTER analysis) and a similarity profile test (SIMPROF) were performed to group sites with similar community composition at 0.1% and 5% significance levels ('simprof' function in *clustsig* package) (Clarke et al. 2008). Principal Component Analysis (PCA) was then used to visualize differences in community composition ('PCA' in *FactoMineR* and 'fviz_pca_biplot' in *factoextra*) (Husson et al. 2010). To display which coral and major benthic categories drove the community differences, correlation vectors were tested for significance ('envfit' in *vegan* with 999 permutations) and overlaid on the PCA plot. Sites were grouped according to wave exposure ($p<0.001$), displayed by concentration ellipses at ellipse.level=0.95. Additionally, impacts of wave exposure on total coral cover, cover of individual benthic categories and rugosity were tested using Welch's t-tests ('t.test' in *base*) to account for unequal variances between groups (Derrick et al. 2016). All statistical analyses were performed using R 4.0.3 (R Core Team 2020).

Pre-bleaching status and recovery trajectories

To determine whether pre-bleaching status and recovery trajectories after the 2015/2016 disturbance event were impacted by wave exposure, we compared the 2020 data to several previous surveys. A similar complete assessment of Salomon's fore reefs was conducted in 2006, taking benthic photographs from the surface at 22 sites (n=1/site) around the atoll at similar locations (Online Resource 1) and depth (6-8 m). These pictures were analysed in CoralNet as described above and benthic cover (accessible at doi) was averaged over sheltered (n=12) and exposed sites (n=10) according to location on the fore reef terrace. Welch's t-tests were used to compare total coral cover and cover of individual categories in 2006 and 2020 ('t.test' in *base*) for both sheltered and exposed sites.

Additionally, cover data for several years between 2006 and 2020 were extracted from published and unpublished datasets to assist analysis of trajectories of coral recovery at both sheltered and exposed sites. These data were collected from a smaller subset of sites (Online Resource 1) and using different methods, but are able to give a broad and general indication of benthic trajectories, as the different benthic survey methods used have been shown to be comparable (Jokiel et al. 2015). Data for 2010 were collected using Point-Intercept transects (n=4/site, 50 m transects, 100 points/transect) at six sites (3 sheltered, 3 exposed) in 8 m depth (Graham et al. 2013). Data for 2016 (2 exposed sites), 2018 (3 sheltered sites) and 2019 (3 sheltered, 3 exposed sites) describe the status of reef communities after the bleaching event and were extracted from video transects in 8-10 m depth (n=3/site, 30 m transect, 60 still images/transect, 10 points/image) for 2016 (Head et al. 2019), 3D line-intercept transects in 8 m depth (n=4/site, 10 m transect, continuous cover along reef contour) for 2018 (Lange and Perry 2019) and 2019 (Lange, unpublished data) and Point-Intercept transects as described above for 2019 (Benkwitt and Graham, unpublished data).

Cover data were averaged over all available replicates of sheltered or exposed sites each year (accessible at doi) before coral community trajectories were visualized using non-metric multidimensional scaling (nMDS) ('metaMDS' function in *vegan* package) (Oksanen et al. 2020). The metaMDS function applied square root transformation and Wisconsin double standardization of cover data before calculating Bray–Curtis dissimilarity. Correlation vectors were overlaid on the nMDS plot, with significant groups indicated on the plot ('envfit' function with 999 permutations).

Results & Discussion

Our study demonstrates that wave exposure is a significant driver of coral reef benthic community composition and recovery trajectories at a remote and uninhabited atoll in the Indian Ocean. In 2020, sheltered reefs along the western shore had significantly higher coral cover and rugosity, while exposed reefs along the eastern shore were characterised by flat, bare pavement and boring sponges. Temporal patterns indicate distinct exposure-driven assemblages with high live coral cover in 2006, extensive coral mortality after the 2015/2016 bleaching event, and ongoing parallel recovery trajectories towards their respective pre-bleaching communities at both sheltered and exposed sites.

Benthic community composition and influence of wave exposure

We found a strong influence of wave exposure on site-level benthic community composition (CLUSTER/SIMPROF and PCA: sheltered versus exposed sites formed distinct groups at p=0.001, Fig. 2b). Differences were driven by relatively high cover of *Porites*, other massive corals, encrusting corals, soft corals, rubble and dead table corals at sheltered sites (each variable contributing >7.5% to PC1) versus high cover of pavement (>7.5%) and sponges (>5%) at exposed sites. Within this broad separation, there were additional sub-groups of statistically distinct benthic communities (CLUSTER/SIMPROF at p=0.05, Fig. 2a). Sites along the NE shore formed a small subgroup within the exposed sites, characterized by relatively high cover of branching *Acropora* and other branching corals (both contributing >7.5% to PC2). Reasons may be a reduction in wave exposure compared to the SE shore, as south-easterly along-shelf currents cross larger distances on the reef terrace, or a weaker exposure to other local-scale physical forcings such as internal tides or patterns of lagoon outflow which could not be accounted for (Williams et al. 2013). Three sites in the sheltered group were characterized by relatively high cover of *Porites* and soft corals, but less rubble or dead *Acropora* tables than at most other wave protected sites, and were therefore likely clustered with the exposed sites in the SIMPROF analysis (Fig. 2a). The other two sites that were isolated in the cluster analysis are located at the southwest corner of the atoll and were characterised by either very high *Acropora* cover or high dead *Acropora* table cover compared to other sheltered sites.

In 2020, sheltered sites had significantly higher coral cover than exposed sites ($t(19.27)=2.55$, $p=0.019$). But while average coral cover along the SE side of the atoll was 8.6% (range: 5.2-17.6%), sites at the NE shore, which were also classified as exposed by the wave exposure model, showed much higher coral cover (mean: 20.3%, range: 13.2-26.2%), similar to averages along the protected NW (mean: 21.6%, range: 14.0-38.6%) and SW shores (mean: 20.1%, range: 19.8-20.4%). Again, this may be explained by lower wave exposure at the NE compared to SE shore. At remote Pacific reefs, horizontal gradients in wave energy explained benthic community patterns and variation in hard coral cover at Kingman Reef, but not at Palmyra (Williams et al. 2013). However, a more detailed nearshore hydrodynamic model around Palmyra captured additional physical forcings and consequently found wave forcing and geomorphology to be major drivers of benthic regimes, especially if hard corals were modelled at the morphology level (Gove et al. 2015).

Substrate rugosity around Salomon atoll was also significantly affected by wave exposure ($t(18.14)=3.65$, $p=0.002$). Markedly low rugosity values were recorded along the exposed SE side of the atoll (range: 1-2), which presently consists of a flat surface of probably pre-Holocene reef rock where all new coral growth gets episodically stripped off during high wave energy events (Grigg 1998). Notable exceptions were the two most eastern stations (2.5 and 3) which were characterized by pronounced spur and groove formations, indicating highest exposure to the main direction of wind-driven swell (Storlazzi et al. 2003; Duce et al. 2016). Rugosity at the remaining sites along the NE, SW and NW side of the atoll ranged from 2-3.5.

Comparing the cover of individual benthic categories, sheltered sites showed higher cover of Porites_massive, Other_massive, Other_encrusting, Soft corals, Rubble and Dead_Acropora_table, while exposed sites were characterized by higher cover of Pavement, Sponge, Sand and Macroalgae (all $p<0.05$). Cover of Acropora_branching, Acropora_table and Other_branching was not significantly different between exposure groups. Previous studies reported that high wave forcing favours wave-tolerant morphologies, such as encrusting and massive corals (Storlazzi et al. 2005; Madin et al. 2006; Gove et al. 2015), which in our study were more abundant at sheltered sites while

Acropora cover was not different between exposures. It is important to remember, however, that Salomon's reefs in 2020 represent assemblages at four years post-disturbance and will inherently differ from mature communities (especially in cover of *Acropora* spp.). The dominance of pavement with low-lying algal species (turf algae and CCA) at high exposure sites on the other hand is consistent with reports from other remote areas (Williams et al. 2013; Gove et al. 2015). Fleshy macroalgal cover in this study was generally very low (<2% at all sites), but significantly higher at exposed than at sheltered sites. This disagrees with observed macroalgae dominance in regions of low wave forcing where vulnerability to physical dislodgement is lowest (Gove et al. 2015), but supports studies finding lower richness, biomass and bite rates of herbivores at highly exposed sites (Karkarey et al. 2020). Dead table corals and rubble were much less prevalent at exposed sites, because they tend to be rapidly removed by high energy monsoonal waves at wind exposed reefs (Yadav et al. 2016).

To summarise, in 2020 the reef structure along the exposed eastern margin of Salomon atoll consisted of a flat surface, in some parts heavily infested by *Cliona* spp. sponges, with relatively small branching and table coral colonies growing on top of it. In contrast, the reef structure along the sheltered western side of the atoll consisted of massive *Porites* colonies, recently dead coral rock which still retained a high structural complexity, and large dead *Acropora* tables, themselves often colonised with juvenile branching coral. This suggests synergistic effects between daily wave exposure and periodic high energy wave events from storms in structuring coral communities, similar to patterns observed around the Hawaiian Islands (Dollar 1982; Grigg 1983; Franklin et al. 2013). Despite the relatively clear impact of wave exposure on community composition, a more detailed nearshore hydrodynamic model and the inclusion of additional physical drivers such as temperature and nutrient concentrations would presumably capture additional physical forcings and may serve as an enhanced tool for exploring biophysical coupling in more detail (Williams et al. 2013; Gove et al. 2015).

Pre-bleaching status and recovery trajectories

A key question arising from the above observations relates to the extent to which reef communities around Salomon atoll differed before the 2015/2016 bleaching event. Our analysis of photographs from 2006 also showed very distinct spatial community patterns, with higher cover of total live coral ($t(19.05)=2.49$, $p=0.022$) and table *Acropora* ($t(15.34)=3.37$, $p=0.004$) at sheltered sites, and higher cover of branching *Acropora* ($t(10.01)=2.94$, $p=0.014$), soft corals ($t(12.05)=2.41$, $p=0.033$) and sponges ($t(9.29)=2.92$, $p=0.017$) at exposed sites (Fig. 3).

It must be noted that reefs in 2006 do not necessarily represent pristine communities, as they reflect conditions eight years after the 1997/1998 bleaching event, when recovery was still ongoing. Coral cover across the Chagos Archipelago actually reached a peak in 2012/2013, after which the dominating large table *Acropora* suffered partial mortality from white band disease (Sheppard et al. 2017). However, the comparison of reef communities in 2006 (8 years post-bleaching) and 2020 (4 years post-bleaching) highlights significant differences. At sheltered sites, total live coral cover decreased from 48.3±6.3% (mean±SE) in 2006 to 6.8±0.8% after the 2015/16 bleaching event (Lange and Perry 2019), but had recovered to 20.5±2.4% by 2020 (42% of 2006 levels; $t(14.08)=4.12$, $p=0.001$). Remaining differences are mainly due to very low cover of tabular *Acropora* (30.8±6.6% in 2006 and 4.1±1.7% in 2020) (Fig. 3). At exposed sites, total coral cover dropped from 29±4.5% in 2006 to 9.9±3.5% in 2016 (Head et al. 2019) and recovered slightly to 12.5±2.1% in 2020 (43% of 2006 levels; $t(12.74)=3.34$, $p=0.006$). As *Acropora* cover was comparatively low even pre-bleaching (branching: 8.8±2.2%, table: 6.4±3.0%), the difference is mainly due to loss of massive *Porites* cover (8.6±2.8% in 2006 to 0.8±0.4% in 2020) (Fig. 3). Dead *Acropora* tables were much less prevalent in 2006 (0.8±0.7%) than in 2020 (10.0±2.0%) at sheltered sites, and generally absent at exposed sites, where degradation of dead reef structure may be faster due to continuously high prevalence of boring sponges and physical substrate stripping. However, differences in rubble and sand cover between 2006 and 2020 were small at all sites (Fig. 3), indicating that the breakdown of reef substrate after the bleaching event is still ongoing (sheltered sites) or that rubble was rapidly transported off-reef (exposed sites).

Adding data from intermediate years, the profound influence of wave exposure on community patterns around Salomon atoll becomes even more apparent. After a benthic community shift from live coral categories in 2006 and 2010 towards high cover of pavement, dead *Acropora* tables and rubble following the 2015/2016 bleaching event, trajectories of coral cover and community composition show recovery trends towards pre-bleaching levels at all sites. Interestingly, the trajectories of reef communities at sheltered and exposed sites are proceeding in a surprisingly parallel way, with reefs in both exposure regimes retaining their distinct communities throughout (Fig. 4).

Figure 4 raises the question of whether exposed reefs are heading towards a new sponge dominated system, but the observed cover of boring sponges in 2006 and 2020 was similar (14.6±4.6% in 2006 and 10.4±2.1% in 2020) and therefore not a result of the recent disturbance. This indicates either a permanently high infestation of the reef framework at exposed sites or an increase in sponge cover after the 1997/1998 bleaching event. The ongoing recovery process towards pre-2015 communities may take longer at wave exposed sites, as the recovery of lost cover of massive corals is slower than that of fast growing *Acropora*. However, coral colonies at exposed sites are generally smaller and coral cover does not reach the same levels as at sheltered sites due to a constant turnover associated with mortality from breakage, scour and abrasion (Grigg 1998; Madin et al. 2006). This indicates that pre-bleaching coral cover levels may actually be reached faster than at sheltered sites. Also, the mechanical stability of settlement structures is critical in determining post-settlement coral survival (Yadav et al. 2016), so the high prevalence of dead *Acropora* tables may slow recovery at sheltered sites as juveniles preferentially settle on this unstable substrate (Arthur et al. 2006; Sheppard et al. 2017).

Future community trajectories

The current status of Salomon's reefs in combination with data from previous years indicates that both sheltered and exposed sites are on a trajectory of recovery to their distinct pre-bleaching communities. Specifically, there is no indication of coral species dominance changes compared to pre-bleaching compositions as reported for some reefs in the central Indian Ocean after the 1997/1998 bleaching event (Arthur et al. 2006; Morri et al. 2015). Consistently low macroalgal cover further suggests that reefs are unlikely to shift to algal-dominated states as observed for several reefs in the more anthropogenically impacted Seychelles after 1998 (Graham et al. 2015). However, most fore reefs in the Central Indian Ocean have low cover of fleshy macroalgae, probably due to high abundance of herbivorous fishes (Arthur et al. 2005; Arthur et al. 2006; Graham et al. 2015; Morri et al. 2015). Similar to other remote reefs in the Indo-Pacific, substrata made available by the death of corals is instead colonised by fine turfing and coralline algae (Gilmour et al. 2013), which are not likely to prevent coral settlement. This is of especially high importance for remote reefs, as without an external supply of recruits, it is assumed that reefs will be slow to recover from severe disturbance (Roberts 1997; Graham et al. 2006; McClanahan et al. 2012) and recruit numbers in the Chagos Archipelago in 2017 were indeed very low (Sheppard et al. 2017). However, we observed high numbers of juvenile *Acropora* colonies around Salomon atoll at both sheltered and exposed sites in 2020, indicating surplus grazing capacity within the system that assisted coral recruitment and survival of locally produced larvae (Mumby and Steneck 2008). This gives reason to hope that reproductive output, recruitment, coral cover and community structure will recover to pre-disturbance levels within a decade as observed for remote Indian Ocean reefs after the 1997/1998 bleaching event (Gilmour et al. 2013; Sheppard et al. 2017). Ultimately, the recovery of reefs in this region will depend on the recurrence intervals and magnitudes of heat stress events in the near future (Van Hooidonk et al. 2016).

Due to its remote environment and absence of direct human impact, Salomon atoll provided a unique opportunity to study the effects of wave exposure on reef benthic community patterns and recovery potential. The distinct communities at sheltered and exposed sites both before and after a major disturbance event confirm the capacity for hard coral assemblages to maintain competitive dominance at an intra-atoll scale in response to wave forcing. Importantly, our results highlight that communities remained distinct during widespread coral loss in 2015/2016 and the following recovery trajectories, and that communities at all sites are on their way to pre-bleaching levels. This emphasises the importance of managing local pressures on reefs to promote natural biophysical coupling and resilience to climate change in the future.

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Data: Site information and benthic cover data from picture analysis and referenced data sets can be downloaded from University of Exeter Repository at doi [*deposited upon acceptance*]

Conflict of Interest: On behalf of all authors, the corresponding author states that there is no conflict of interest.

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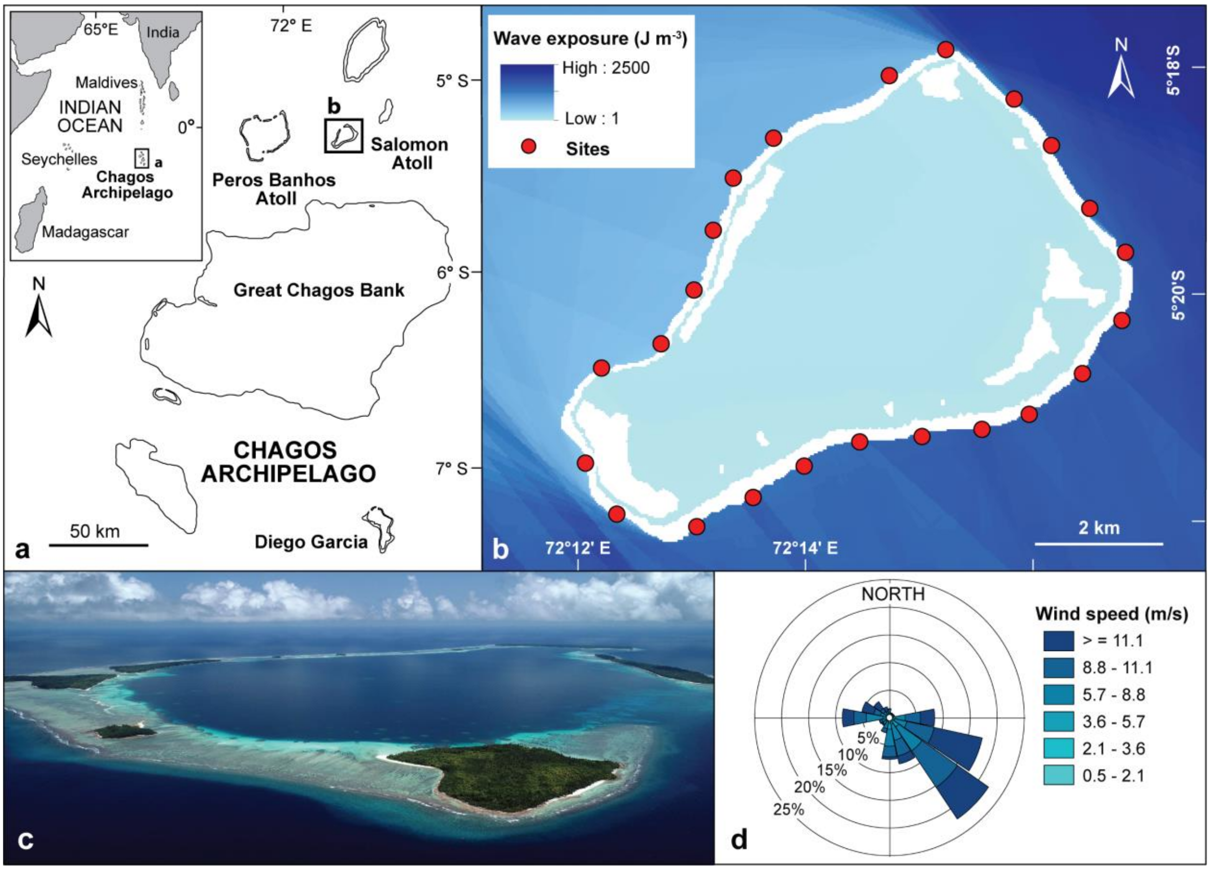

Figure 1: Location of study sites. a) Location of Salomon atoll in the Chagos Archipelago and in the central Indian Ocean (inset); b) Modelled wave exposure around Salomon atoll with locations of 23 surveyed fore reef sites (in red); Blue shading indicates magnitude of wave exposure; c) Drone image of Salomon atoll from the most northern point looking south (channel into the lagoon on the right), photo courtesy of Robert Dunbar; d) Rose diagram showing annual wind direction, frequency and speed based on hourly wind measurements obtained from Diego Garcia airport (adapted from Perry et al. 2015).

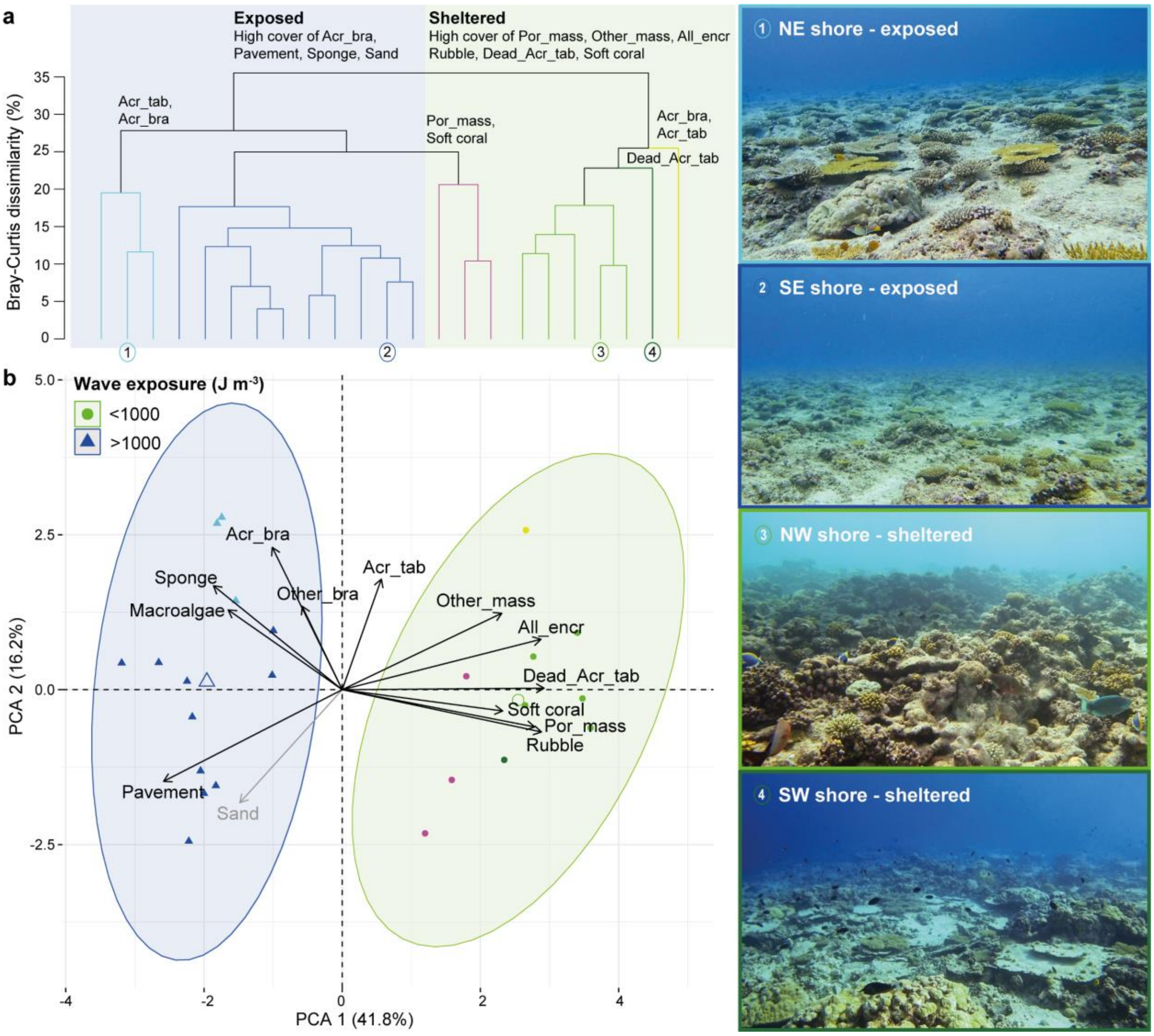

Figure 2: Reef community composition around Salomon atoll. a) CLUSTER/SIMPROF Analysis indicating significant differences in community composition among sites at a significance level of p=0.05 (colored lines). Wave exposure (blue box: exposed >1000 J m^{-3}, green box: sheltered <1000 J m^{-3}) and categories driving the differences were added post analysis; b) Principal Component Analysis (PCA) showing similarities in community composition in a two-dimensional space with sites colored according to SIMPROF Cluster Analysis and symbols and ellipses denoting the gradient in wave exposure (at p=0.001; blue: exposed, green: sheltered; empty symbols represent center points of ellipses). All benthic vectors except 'Sand' significantly drive the displayed differences between sites (at p<0.05); Abbreviations: Acr – Acropora, Por – Porites, bra – branching, tab – table, mass – massive, encr – encrusting. Photographs in the right panel show reef community and structure at exposed and sheltered sites indicated by colored frames and numbers 1-4.

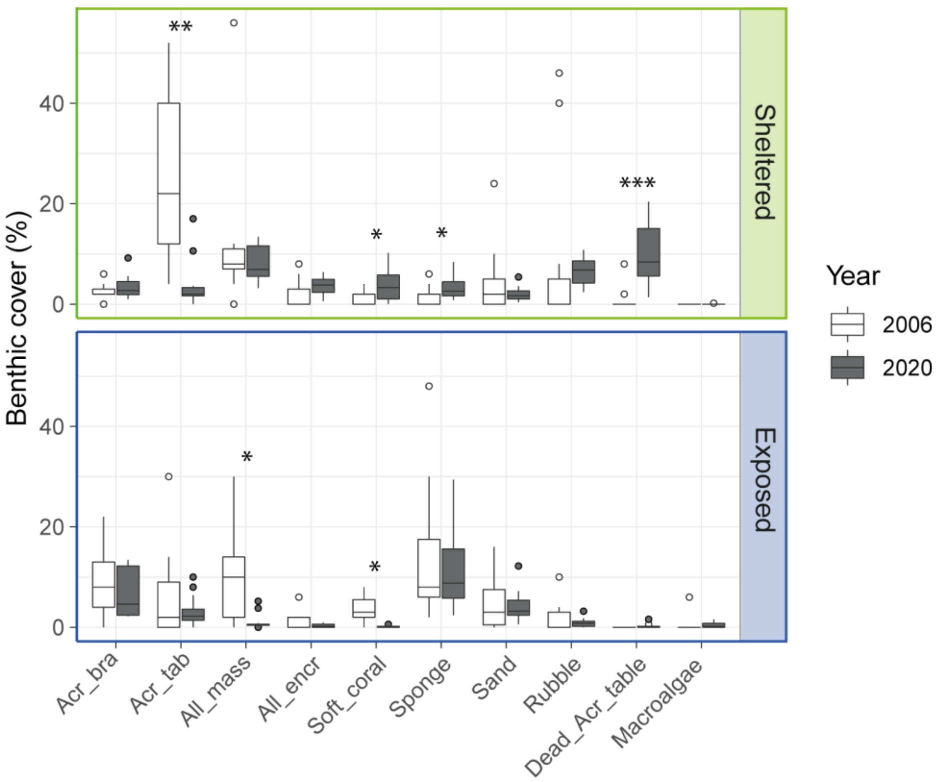

Figure 3: Percent cover of main benthic categories at sheltered and exposed sites in 2006 and 2020. Note that All_mass includes Porites_mass and Other_mass and that Pavement was not plotted (2006: 36±5% (mean±SE) at sheltered and 45±4% at exposed sites; 2020: 53±8% at sheltered and 71±10% at exposed sites). Abbreviations: Acr – Acropora, Por – Porites, bra – branching, tab – table, mass – massive, encr – encrusting. Boxes depict 25th and 75th percentiles with median line, whiskers and points extend to the smallest and largest values. Results of Welch's t-tests are stated if significant (***<0.001, **<0.01, *<0.05).

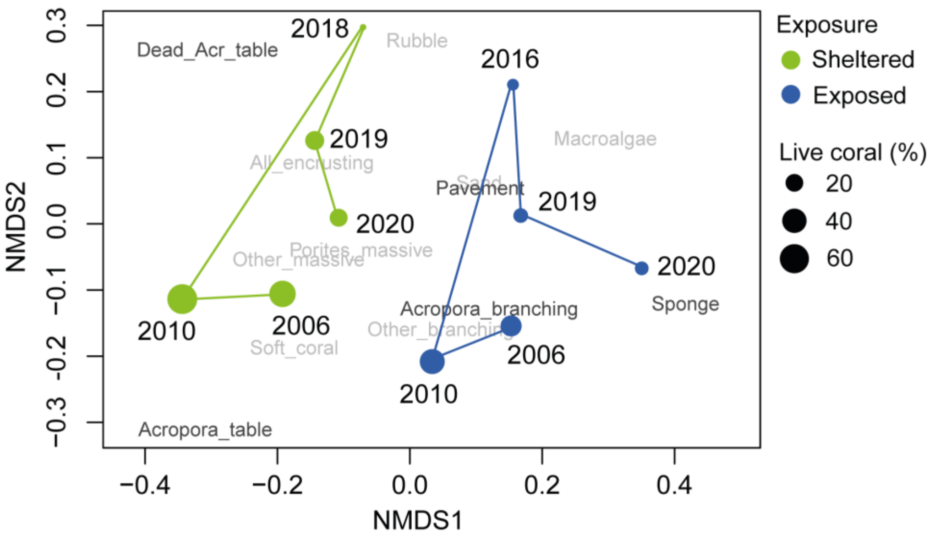

Figure 4: Non-metric multidimensional scaling (nMDS) of benthic communities between 2006 and 2020 at sheltered (<1000 J m^{-3}; green) and exposed (>1000 J m^{-3}; blue) fore reefs around Salomon atoll. Vectors connecting years display directional change of coral community composition. Benthic groups driving differences among locations and years are displayed in grey (dark grey *p*<0.05, light grey *p*>0.05). Scaled points indicate mean percent hard coral cover per year.